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BRIEFER ARTICLES.

HABERLANDT'S NEW ORGAN ON CONOCEPHALUS.¹

PROFESSOR HABERLANDT'S contribution to the Schwendener *Festschrift* is an argument based upon previously published data.² in which he arrives at conclusions of such great importance, if well founded, that further discussion is certainly worth while. Let us begin with a statement of the facts in the case, in which literal quotations are made from the *Festschrift*.

The subject, *Conocephalus ovatus*, is a Javanese liane, with large, leathery leaves. On its upper surface are some hundred "Scharf differenzirte Epithem-Hydathoden mit Wasserspalten." "Bei keiner anderen Pflanze war die nächtliche Wasserausscheidung seitens der Hydathoden so constant und schön zu beobachten, wie bei der in Rede stehenden Liane." In a concrete case, a leaf ejected 26 per cent. of its own weight in water, in one night. When these hydathodes are poisoned, with 1 per cent. alcoholic corrosive sublimate, the excretion of water ceases. The next morning the leaf is dry outside, but there is "Eine oft sehr weitgehende Injection der Durchlüftungsräume mit Wasser." The water gradually disappeared, with active transpiration during the forenoon. This was repeated for three or four days; then there was a new response. "Auf den bepinselten Blatthälften entstanden nämlich zum Ersatze der vergifteten Hydathoden ganz neue Wasserausscheidungsorgane von wesentlich anderem histologischen Bau und anderer entwicklungsgeschichtlicher Herkunft, wie sie im normalen Entwicklungsgange der Pflanzen niemals auftreten." On subsequent mornings, drops were found on these structures, and the intercellular spaces were not injected. "Die neugebildeten Organe waren also vollkommen im Stande, die getödteten Epithem-Hydathoden in ihrer Funktion zu ersetzen."

¹ HABERLANDT, G., Ueber experimentelle Hervorrufung eines neuen Organes bei *Conocephalus ovatus* Tréc. Bot. Untersuchungen S. Schwendener dargebracht. Berlin, 1899.

² HABERLANDT, G., Ueber wassersecrenirende und-absorbirende Organe. Sitzber. Ak. Wiss. Wien. 1:55. 1895.

The substitute hydathodes are formed only where trichome clusters have given place to colleters, and the cuticle has been elevated and then split by mucilage. In their formation the tissue first concerned is the parenchyma of the bundle sheath, which enlarges greatly, breaks through the overlying tissues, and finally grows out into "Farblosen Haaren, die pinselförmig auseinander treten." The neighboring palisade parenchyma may share in this formation. The excretion of water is presumed to be, as in normal hydathodes, an active process. "Nachdem sie ungefähr eine Woche lang allnächtlich Wasser ausgeschieden haben, gehen sie allmählich zu Grunde." After their death, the leaf "Lässt auf seiner Unterseite durch Wucherungen der Epidermis und namentlich der darunter befindlichen Wassergewebsschicht zahlreiche ein- und mehrzellige Wasserblasen entstehen."

Haberlandt's argument from these data may be epitomized as follows. The substitute hydathodes are real *organs*, and not accidental structures, or purposeless results of injury to the plant, because they occur in particular places and are strikingly differentiated (the structural argument), and get rid of the plant's excess of water (the physiological argument). They are *new* organs because no similar structure is known on any part of *Conocephalus* or any related plant. Natural selection cannot have produced them because the occasion for them does not arise in nature; no known natural agent destroys the normal hydathodes, and they remove all the surplus water at the height of the rainy season. And natural selection would have made the substitute hydathodes reasonably permanent, instead of transitory. Summing up, so far, "Ein neues, zweckmässig gebautes und funktionirendes Organ ganz plötzlich, ohne früheres Vorbandensein einer rudimentären Anfangsbildung, ohne Vermittlung von sich allmählich vervollkommnenden Uebergangsstufen, und ohne die geringste Mitwirkung der Naturzüchtung entstehen kann. Bei der Erklärung des Zustandekommens der geschilderten Ersatz-Organversagt die Selectionstheorie vollkommen ihren Dienst." The inadequacy of the theories of Nägeli and Weismann to explain completely the phenomenon is then shown; but a plausible solution based on them is reached. "Wenn nun auch ein besonderer Anlagenkomplex, eine eigene Determinante für diesen neuen Typus von Hydathoden im Idioplasma unmöglich vorhanden sein kann, so lässt sich doch wahrscheinlich machen, dass die einzelnen Elemente dieses Anlagenkomplexes im Idioplasma vertreten sind. Die Ersatz Hydathoden bestehen in ihren wesentlichsten Theilen aus

haarförmigen Schlauchzellen, denen die Fähigkeit einseitiger Wasserauspressung zukommt; sie verhalten sich also wie Wurzelhaare, die ja gleichfalls im dampfgesättigten Raume nicht selten die Fähigkeit besitzen, kleine Wassertröpfchen auszusecheiden. Nehmen wir nun an, dass in den Zellkernen der Leitparenchym, Palissaden- und Wassergewebszellen, die zu den Schlauchzellen der Ersatz-Hydathoden auswachsen, die idioplasmatische Anlage zur Haarbildung in Kombination mit der Anlage zu der eine einseitige Wasserauspressung ermöglichenden Struktur der Plasmahaut in Aktion tritt-Anlagen die im Idioplasma unserer Pflanze jedenfalls vertreten sind so erscheinen damit wenigstens die wichtigsten Voraussetzungen für die Entstehung der Ersatz-Hydathoden in der Struktur des Idioplasmas von vornherein gegeben."

If I have left any unclearness in Haberlandt's argument the fault is mine; it is not in the original. From the point where the new structure is recognized as a substitute hydathode, formed to relieve the plant of its surplus water, there is no escaping the conclusion that the theory of natural selection is inadequate and faulty. Nor is this all. Haberlandt concludes: "Ob man aber mit Rücksicht darauf, dass jene Entwicklungsvorgänge zur Entstehung eines *zweckmässig* gebauten und funktionirenden Organes führen, welches ganz ausserhalb des Bereiches der Naturzuchtung liegt, das Walten einer 'Entwicklungsintelligenz' annehmen soll, das zu entscheiden ist Sache des rein subjektiven Ermessens und Bedürfnisses jedes einzelnen. Die Naturforschung hat mit derlei metaphysischen Weiterungen nichts zu thun." But if we follow Haberlandt as far as he leads, we must balk sheer, or take the only remaining step of accepting the evidence of a design. And as surely as teleology is the natural enemy of modern science, it is a real concern of scientists whether or not they furnish material for its exponents. It seems to me that if Haberlandt's data admit of an interpretation freer from teleology, and otherwise more in harmony with the behavior of other plants, the more commonplace interpretation will commend itself.

Haberlandt's *dictum* that in judging the character of a new structure, "Nicht bloss die histologische und physiologische Beschaffenheit der sie aufbauenden Elemente, sondern ebenso sehr auch die jeweilige Kombination dieser Elemente in Betracht kommt," is a help to the clearest view of it only when the function does not follow directly from the structure, and when the units of structure are diverse in development. But when the performance of the function follows

obviously from the structure, and when all structural units are evidently formed in response to a common stimulus by a similar course of growth, then the introduction of the combination of elements as a feature distinct from the elements themselves is superfluous and cumbersome. In this case all the structural elements are similar hair-shaped cells, as stated in two quotations above ; that the stimulus to the formation of them all was the excess of water hardly admits of question. Formed from the original cells which do give rise to them, any essentially different arrangement or combination of these elements from that occurring is not conceivable. That is, the existing combination of the histological elements follows from their origin. The intimate connection of the histological and physiological features is constantly emphasized by Haberlandt ; his whole argument involves this, the "Zweckmässigkeit" of the structure. It is possible that the action of the substitute hydathode follows from its structure even more intimately than Haberlandt explains. There is nothing difficult to believe in his supposition that the excretion of water is active on the part of the cells.³ Such one-sided activity may be manifested in the endodermis or other cells which force water into the xylem of all plants in which there is root pressure. And it would be only an assumption of a power of the epithem, analogous to many familiar correlations. But even this use of normally dormant determinants is not altogether necessary. Haberlandt says, "Auch eine passive Druckfiltration durch die lebenden Zellen der Ersatz-Hydathode ist nicht anzunehmen, da nicht einzusehen wäre, weshalb durch die turgeszirenden Hydathodenkörper das Wasser leichter durchgepresst werden sollte, als durch die lebenden Parenchymseiden der Gefässbündel." Very thin walls and protoplasmic linings inside them would suggest easy filtration under pressure ; these are characters of the oedemata of tomato to be mentioned presently, and presumably of the structures in question on *Conocephalus*. More important than visible difference in the structure is difference in the turgor. As I have repeatedly shown,⁴ the more rapidly cells grow, the less their turgor becomes. In the hypertrophied cells of the substitute hydathode there must be a very much lower osmotic pressure than in the cells from which they grew. The hydrostatic pressure in the tracheides at night exerts an equal force to

³ Assuming, what is open to suspicion, that normal hydathodes act in this way.

⁴ Ueber den Einfluss von Licht und Temperatur auf den Turgor. Halle a. S. 1896.

drive water through the bundle sheath into the intercellular spaces, and through the substitute hydathode into the free air ; but the pressure thus exerted is much less in proportion to the osmotic pressure to which the protoplasm is accustomed in the bundle sheath. It might be anticipated then that through the substitute hydathode, where the excess pressure is relatively great, the water would escape.

After what has been said, I think it will be agreed that, given the structure of the substitute hydathodes as it is, there is nothing very surprising or remarkable in their behavior. It remains, then, to show that the structure is essentially similar to such as the same condition produces in many plants. The condition is excess of moisture. The chief characteristic of the structure is great hypertrophy of a group of cells.

Two years before Haberlandt first published his account, a paper appeared by Atkinson⁵ on oedema of the tomato. When tomato beds in the forcing house were warmed so that root pressure furnished water faster than it transpired, or when water was forced into branches by connection with a faucet, these oedemata were developed. In my laboratory, Mr. T. C. Johnson caused their formation readily by forcing water into cut branches under a moderate head of mercury. The observations agreed entirely with Atkinson's, whom I therefore quote : "The epidermal cells were very much enlarged, while the chlorophyll bearing cells just beneath, as well as some of the more deeply seated cells, were greatly elongated in a radial direction, and strongly clavate at their outer extremity where this extended beyond the lateral pressure from adjacent tissue. In many cases the epidermal cells quickly separate and slough off. The cells of the affected areas possess exceedingly delicate walls, so that with little disturbance they would collapse. There was little protoplasm in proportion to the size of the cell and a corresponding amount of cell sap." "The increase in the number of cells in such cases," *i. e.*, when there is an increase, "occurs simply by the formation of transverse walls in the elongated cells." Later Atkinson speaks of "stretching of groups of cells to eight to ten times their normal size." The oedemata appear on the veins of the lower surface of the leaf blade (rarely on the upper surface), on the midrib, petiole, and stem. When water is forced into branches it emerges as drops along the edges of the leaves, or elsewhere, if any injury affords an

⁵ATKINSON, G. F., Oedema of the tomato. Rep. Agr. Exp. Stat., Ithaca, N. Y. 1893, pp. 101-128.

opportunity ; to some extent the intercellular spaces become charged. In Atkinson's experiments the plants became wet ; it probably did not occur to him to look for the extrusion of water from the sounder oedemata. In our experiments, instituted to see if this took place, the oedemata merely became wet when evaporation was prevented ; drops of water were not excreted by them, however freely they might be forced out along the margin of the leaf. Evidently, though water can be forced through them, they are passive in the process, and the water escapes the easier way. But Atkinson says that water is set free by the collapse of hypertrophied cells : "The changes brought about by the escape of water from this and adjacent tissues during the warmer parts of the day may be so profound as to cause the leaf to wilt and die."

On the tomato then we have the same abnormal condition which caused the formation of the substitutes hydathodes of *Conocephalus*, producing structures which are like them in being formed on the veins, and in being formed from a group of cells of various tissues, which become tubular and segment below, and swell up at the free end ; without doubt there are other details of resemblance—as in the thin walls and scanty protoplasm. Unquestionably, the two structures are homologous ; but on the tomato the oedemata excrete little water, or the loss injures the plant. Their appearance is a pathological phenomenon, whose cause is clear ; to seek to discover a purpose for them would be fatuous. Natural selection has provided the plant with responses to many frequently recurring pathological conditions. The ancestors of *Conocephalus* were always liable to mechanical injuries, and those whose wounds healed had in such cases an advantage ; so the final cutting off of the substitute hydathodes by a callus may be ascribed to natural selection. But such exigencies as the loss of the hydathodes must have occurred to *Conocephalus* practically as rarely as corrosive sublimate entered them. Of course, natural selection is not responsible for the results. On grounds that we cannot yet elucidate well, even in theory, the hydathode responds to the corrosive sublimate by dying, and the leaf responds to the excess of water by the hypertrophy of groups of cells. The relation of cause and effect is equally clear, the details equally mysterious, in the two cases. We should see a purpose in both or neither. If the "Ersatz-Hydathode" admits of construction as evidence of the reign of an "Entwicklungs-intelligenz," the fatal action of corrosive sublimate must make us suspect the presence of a power of evil.

Science cannot make a discrimination between the structures on *Conocephalus* and tomato. Both must be regarded as oedemata, and it is merely incidental that those of *Conocephalus* temporarily furnish the easiest avenues for the escape of water under pressure. Haberlandt tells us truly that drops of water can be forced out through root hairs. That happens when the root is in the same condition as the *Conocephalus* leaves. It does not illustrate a "Zweckmässigkeit" on the part of the root hairs. It does not entitle them to be regarded as organs of excretion, emergency hydathodes. But there is only the same ground for calling the *Conocephalus* oedemata "organs," when they are of incidental temporary utility.

The position of the "substitute hydathodes," which Haberlandt regards as a striking feature, has not been discussed. They must be formed on the veins, because, as in the tomato, the water is most excessive there. And their appearance under old collaters is at the points of least resistance, where the cuticle is already ruptured and the walls have been partly softened. Atkinson says that oedemata on the tomato stem are formed in places where there are already large cells and "their walls are less resistant." If the oedema cells are even more slender in *Conocephalus*, as the figures would indicate, it is what should be anticipated from the firmer texture of the leaf.

The tomato has so far been used alone to furnish another instance parallel to that of *Conocephalus*, because it has been well worked out, and is an especially easy subject for such experiments. There are numerous other known illustrations. Haberlandt mentions the fact that Sorauer describes "Pathologische Veränderungen der Laubblätter verschiedener Pflanzen, welche mit dem Bau der Ersatz-Hydathoden von *Conocephalus* eine gewisse Aehnlichkeit besitzen." After remarking the absence of proof that these structures are caused by excess of water (which proof has been given for the tomato), Haberlandt grants that they may be "Analoge Erscheinungen . . . unvollkommene Ansätze zu einer Selbstregulation, die bei unserer Pflanze ganz unvermittelt in so vollkommener Weise sich einstellt."

Excessive moisture acts in the same way elsewhere than on leaves. Atkinson⁶ describes an oedema on apple branches, resultant from excessive pruning and subsequent congestion with water. Their appearance on tomato stems has been mentioned. Ward (cited by

⁶ ATKINSON, G. F., Oedema of apple trees. Rep. Agr. Exp. Stat., Ithaca, N. Y., 1893. pp. 305-307.

Atkinson) has reported them on potato stems. Devaux⁷ describes oedemata on potato tubers kept saturated; they naturally appeared where the resistance to their growth was least—at the lenticels. Tubeuf⁸ has reported what is doubtless the same result of excessive moisture on trees. They may also occur on roots in water.⁹ Von Mohl¹⁰ describes such structures formed under the influence of moisture from the lenticels and cortical parenchyma of *Salix viminalis* branches.

In plants whose normal habitat is wet, there has been an opportunity for natural selection to develop and utilize the excessive growth of the cells under the influence of water; and the utilization has been in several ways. The most common of these adaptations is aerenchyma.^{11, 12} The oedemata of the lenticels of stems serve to connect perfectly the normal aerenchyma of water plants with the oedemata of leaves. It is a matter for individual judgment when it should be regarded as in the nature of a disease, and when as a normal structure. Even in water plants (Goebel *et al.*) its formation depends on the moisture and can be artificially regulated. It is not unusual for structures pathological in one plant to be normal in another. But no structure can be regarded as normal on a plant where it occurs too rarely for it to be subject to development by natural selection.

Goebel seems entirely justified in deriving the excessively light and porous tissue of *Aeschynomene* and other plants in water from aerenchyma. In these this tissue serves as a float. It is formed in the leaf of *Desmanthus* (*Neptunia*) *natans*, the petiole of the water hyacinth (*Eichhornia*), the stem of *Nesaea*,¹³ and the root of *Sesbania*.¹⁴ The

⁷ DEVAUX, H., Hypertrophie des lenticelles chez la pomme de terre et quelques autres plantes. B. S. B. France. 38: 48-50. 1891.

⁸ TUBEUF, C. v., Ueber Lenticellen-Wucherungen (Aerenchym) an Holzgewächsen. Forst.-Naturw. Zeits. 405-414. 1898; Rev. in Bot. Centralb. 77: 369.

⁹ SCHRENK, H. v., Oedema in roots of *Salix nigra*. BOT. GAZ. 24: 52. 1897.

¹⁰ Verm. Schriften 259-332. Flora, 1832.

¹¹ SCHENK, H., Ueber das Aerenchyma, ein dem Kork homologes Gewebe bei Sumpfpflanzen. Jahrb. Wiss. Bot. 20: 526-574. 1889.

¹² GOEBEL, K., Pflanzenbiologische Schilderungen II. 2. Die Wasserpflanzen. Marburg. 1893, p. 256 ff. Fig. 69 is abnormal aerenchyma (oedema) in the lenticels, of *Populus nigra*.

¹³ SCHRENK, J., On the floating tissue of *Nesaea verticillata*. Bull. Torr. Bot. Club. 16: 315. 1889.

¹⁴ SCOTT, D. H. and WAGER, H., On the floating roots of *Sesbania aculeata* Pers. Annals of Botany 1: 307-314. 1888.

water acts on as various tissues to form these floats as are hypertrophied by it in oedemata.

I have not intended to cite any large part of the literature on this subject. For a fuller review of it Sorauer's *Pathology* and the work of Atkinson, Goebel, and Schenk referred to here should be consulted. The cases cited here are sufficient to show that excessive moisture produces on various parts of a great many plants structures essentially similar to those it causes on the leaf of *Conocephalus*.

A long list of cases similar to this is contained in a more recent paper by Sorauer,¹⁵ in which he comes to the same conclusion with regard to *Conocephalus* that I have reached independently. Another very recent piece of work is by Miss Dale,¹⁶ who finds that if other conditions are suitable moisture stimulates the formation of "hypertrophied outgrowths of epidermal cells, beginning at a stoma;" sometimes the underlying cells are also influenced. Her description and figure would fit almost perfectly for the raised stoma at the base of the hypocotyl of *Lupinus* (BOT. GAZ. 31: 413). From the fact that the same conditions of moisture which determine their development at the base of the hypocotyl (where the environment is normally very moist, or the seed would not germinate) do not give rise to them elsewhere on *Lupinus*, it seems likely that they are a product of natural selection and have a function — probably the increase in gas exchange with the air in or very near the ground. Miss Dale satisfies herself that the *Hibiscus* intumescences are pathological, but then looks for a function for them, suggesting that "they may be a sort of abnormal organ for the direct excretion of water." But they do not seem to have been observed to excrete it. From her results with *Hibiscus* and *Ipomoea*, she suggests that the "Wasserblasen" of Haberlandt's subject occurred on the nether surface of the leaf because the stomata are there.—EDWIN BINGHAM COPELAND, *Hull Botanical Laboratory, Chicago*.

¹⁵ SORAUER, P., Ueber Intumescenzen. Ber. Deutsch. Bot. Gesell. 17: 456-460. 1899.

¹⁶ DALE, ELIZABETH, Investigations on the abnormal outgrowths or intumescences on *Hibiscus vitifolius* L. Phil. Trans. Roy. Soc. London. Bot. 194: 163-182. 1901; also a note in Bot. Centralb. 85: 372-375. 1901.